

Replica symmetry breaking in an adiabatic spin-glass model of adaptive evolution

Ayaka Sakata,^{*} Koji Hukushima,[†] and Kunihiko Kaneko[‡]

*Department of Basic Science, Graduate School of Arts and Sciences,
The University of Tokyo, Komaba, Meguro-ku, Tokyo 153-8902, Japan.*

(Dated: November 28, 2011)

We study evolutionary canalization using a spin-glass model with replica theory, where spins and their interactions are dynamic variables whose configurations correspond to phenotypes and genotypes, respectively. The spins are updated under temperature T_S , and the genotypes evolve under temperature T_J , according to the evolutionary fitness. It is found that adaptation occurs at $T_S < T_S^{\text{RS}}$, and a replica symmetric phase emerges at $T_S^{\text{RSB}} < T_S < T_S^{\text{RS}}$. The replica symmetric phase implies canalization, and replica symmetry breaking at lower temperatures indicates loss of robustness.

PACS numbers: 87.10.-e, 75.10.Nr

Biological evolution occurs through changes in genotypes and phenotypes over generations, driven by random genetic variance and natural selection. This process preferentially selects genotypes that produce a phenotype that affords high evolutionary fitness [1, 2]. Thus, phenotypes, such as protein expression levels or the functional structures of proteins, are the result of dynamic processes governed by the genes. However, such processes generally involve stochasticity due to thermal noise, and thus phenotypes of isogenic individuals are not necessarily identical [3–5]. Indeed, such phenotypic fluctuations and the possible role of noise have been extensively investigated both experimentally [6, 7] and theoretically [8–10].

For a phenotype to conserve its function, however, it must be robust to this noise, at least to some degree. Indeed, the dynamic adaptation process that shapes phenotypes exhibits global and smooth attraction, as observed in the folding dynamics of proteins [11, 12], RNA [13], protein expression dynamics governed by gene regulatory networks [14], developmental dynamics [15], and so forth. Besides this robustness to noise, the adapted phenotype should be robust to genetic change to acquire evolutionary stability. The possible relationship between these two types of robustness, as well as the positive role of noise, has recently been investigated theoretically [8–10, 13, 16]. The study found a transition toward robustness in the dynamic process with respect to the noise level (temperature), where the energy landscape for the dynamics changes from being rugged to having a funnel-like structure.

Considering the above change in the dynamical process, one may expect that loss of robustness could be viewed as a transition to the spin-glass phase in statistical physics. Thus far, however, no analytic theory to

support this view has been provided, and, from a theoretical standpoint, little is understood of this transition in the evolution of robustness against noise (temperature).

Here we introduce a simple statistical-mechanics model of adaptive evolution to explain the dynamical process that shapes phenotypes. We use an adiabatic two-temperature spin-glass model in which the spin configuration and the interaction matrix correspond to the phenotype and genotype, respectively. The genotype evolves to increase fitness which is defined by the spin configuration. With an analysis based on replica theory, we demonstrate the emergence of a replica-symmetry-breaking transition as the temperature decreases, and show that the transition corresponds to a loss of robustness in the phenotype. Adaptive evolution of robustness is shown to occur only in the replica symmetry phase, where the Hamiltonian for global attraction to the adapted phenotype is represented in terms of frustration. We also discuss the significance of replica symmetry breaking on phenotypic robustness.

Let us consider a simple spin model in which the phenotype and genotype are represented by configurations of spin variables $\mathbf{S} \equiv \{S_i\}$ and the interaction matrix elements $\mathbf{J} \equiv \{J_{ij}\}$, respectively, with $i, j = 1, \dots, N$. Each spin variable S_i can take one of two values, ± 1 . The interactions are fully connected between two spins. Both the spins \mathbf{S} and interactions \mathbf{J} are treated as dynamical variables, but the time scale associated with \mathbf{J} is much slower so that the interactions are relatively fixed during the time evolution of the spins. Thus, the equilibrium distribution of the spins is given by $P(\mathbf{S}|\mathbf{J}) = \frac{1}{Z_S(\mathbf{J})} \exp(-\beta_S H(\mathbf{S}|\mathbf{J}))$, where $\beta_S = T_S^{-1}$, the Hamiltonian is given by $H(\mathbf{S}|\mathbf{J}) = -\frac{1}{\sqrt{N}} \sum_{i<j} J_{ij} S_i S_j$, and $Z_S(\mathbf{J})$ is a partition function under a given \mathbf{J} . Within the long evolutionary time scale for \mathbf{J} , the spin configuration driven by a Hamiltonian H_J reaches thermal equilibrium. The distribution function of \mathbf{J} is given by $P(\mathbf{J}) = \frac{1}{Z_J} \exp(-\beta_J H_J(\mathbf{J}))$, where $\beta_J = T_J^{-1}$ and Z_J is the total partition function. The function H_J is generally expressed in terms of equilibrium quantities of \mathbf{S} and a bare distribution $P_0(\mathbf{J})$. Here we set the Hamiltonian of

^{*} ayaka@sp.dis.titech.ac.jp; Present address: Department of Computational Intelligence and Systems Science, Tokyo Institute of Technology, Midori-ku, Yokohama 226-8502, Japan.

[†] hukushima@phys.c.u-tokyo.ac.jp

[‡] kaneko@complex.c.u-tokyo.ac.jp

\mathbf{J} as

$$H_J(\mathbf{J}) = -\Psi(\mathbf{J}) - T_J \log P_0(\mathbf{J}), \quad (1)$$

where $\Psi(\mathbf{J})$ is a fitness function. The bare distribution is given by $P_0(\mathbf{J}) = \prod_{i < j} \frac{1}{\sqrt{2\pi}} \exp(-J_{ij}^2/(2J_0^2))$, with a unit J_0 of the interaction. We assume that fitness is determined by a specific configuration of given t spins, called target spins here. (For example, protein function depends on the conformation of a set of residues, and is indeed modeled by the configurations of target spins in [16]). More specifically, we assume that a functional phenotype is generated when the configurations of target spins satisfy $\sum_i^t S_i = t\mu$ with μ being a constant value. The remaining $N - t$ spins, called non-target spins, have no direct influence on the selection of individuals. The fitness function is thus defined by

$$\Psi(\mathbf{J}) = \log \left\langle \delta \left(\mu, \frac{1}{t} \sum_{i=1}^t S_i \right) \right\rangle \equiv \log \langle \psi(\mathbf{S}) \rangle, \quad (2)$$

where δ is Kronecker's delta and $\langle \cdots \rangle$ is the thermal average with respect to the spin variables according to the equilibrium distribution. The fitness function $\Psi(\mathbf{J})$ implies a logarithmic probability for the magnetization of t -spins to take the value μ in equilibrium. Note that it does not matter which spins are chosen as targets because the model is a fully-connected mean-field model. The configuration of t -spins is not important either, because of the gauge symmetry, which guarantees that a system with any configuration of t -spins can be transformed into the system studied here, without altering the thermodynamic properties [17]. The equilibrium distribution of \mathbf{J} and the total partition function are written as

$$P(\mathbf{J}) = \frac{1}{Z_J} P_0(\mathbf{J}) \langle \psi(\mathbf{S}) \rangle^{\beta_J}, \quad Z_J = [\langle \psi \rangle^{\beta_J}]_0, \quad (3)$$

where $[\cdots]_0$ means the average over \mathbf{J} with respect to the bare distribution $P_0(\mathbf{J})$. When $T_J = \infty$ or $t = 0$, the distribution $P(\mathbf{J})$ is identical to $P_0(\mathbf{J})$ irrespective of their fitness values, and the system corresponds to the Sherrington-Kirkpatrick (SK) model. For finite T_J and t , the interactions \mathbf{J} that frequently lead to the spin configuration with $\sum_{i=1}^t S_i = t\mu$ appear with higher probability. In this sense, the temperature T_J plays the role of the selection pressure in genotypic evolution.

Assuming that β_J is a positive integer, the quantity $\langle \psi(\mathbf{S}) \rangle^{\beta_J}$ can be expressed in terms of β_J real replicas. Following the replica method [18], the total partition function Z_J can be expressed as

$$Z_J = \lim_{n \rightarrow 0} \int D\mathbf{J} P_0(\mathbf{J}) \text{Tr}_{\{\mathbf{S}^\alpha\}} \prod_{\alpha=1}^{\beta_J} \psi_\alpha e^{-\beta_S \sum_{\gamma=1}^n H_\gamma}, \quad (4)$$

where $\psi_\alpha = \psi(\mathbf{S}^\alpha)$ and $H_\alpha = H(\mathbf{S}^\alpha | \mathbf{J})$. The right hand side of eq. (4) is originally calculated for a positive integer n and β_J while keeping β_J smaller than n , and then the

partition function Z_J is analytically continued to non-integer β_J and non-integer n with the limit to 0. After some calculations, the total free energy can be derived as a function of replicated order parameters $\{q_{\alpha\beta}\}$, their conjugate parameters $\{\hat{q}_{\alpha\beta}\}$, and parameters $\{\hat{\mu}_\alpha\}$ conjugated with μ , which are determined by self-consistent equations. The replicas from the first to β_J -th are subjected to the external field ψ_α , and the others are not. Taking the difference in the replicas into account, we introduce a replica symmetric (RS) assumption for $q_{\alpha\beta}$ as

$$q_{\alpha\beta} = \begin{cases} q_1, & \text{if } \alpha \leq \beta_J, \beta \leq \beta_J \\ q_2, & \text{if } \alpha \leq \beta_J, \beta > \beta_J \text{ or } \alpha > \beta_J, \beta \leq \beta_J \\ q_3, & \text{if } \alpha > \beta_J, \beta > \beta_J. \end{cases} \quad (5)$$

For the conjugate parameters $\{\hat{\mu}^\alpha\}$, it is assumed that $\hat{\mu}_\alpha = \hat{\mu}$ for any $\alpha \leq \beta_J$. With these assumptions, the RS total free energy density f_{RS} is given by

$$\begin{aligned} f_{\text{RS}}(T_S, T_J, \mu) = & -p\mu\beta_J\hat{\mu} - \frac{\beta_J\beta_S^2(q_1 - q_3)}{2} \\ & - \frac{\beta_S^2}{2} \left(\frac{\beta_J(\beta_J - 1)q_1^2}{2} - \beta_J^2 q_2^2 + \frac{\beta_J(\beta_J + 1)q_3^2}{2} \right) \\ & + (1 - p) \log \Xi(0) + p \log \Xi(\hat{\mu}), \end{aligned} \quad (6)$$

where $p = t/N$. Here $\Xi(w)$ is defined as a normalization constant of the distribution

$$P(u, v; w) = \frac{e^{-(u^2+v^2)/2}}{2\pi\Xi(w)} \left(\frac{\cosh(w + \sqrt{\hat{q}_1}u)}{\cosh W(u, v)} \right)^{\beta_J}, \quad (7)$$

where $W(u, v) = \sqrt{\frac{\hat{q}_2}{\hat{q}_1}}u + \sqrt{\frac{\hat{q}_1\hat{q}_3 - \hat{q}_2^2}{\hat{q}_1}}v$; and \hat{q}_1 , \hat{q}_2 , and \hat{q}_3 are the conjugate parameters of q_1 , q_2 , and q_3 , respectively. At $\mu = 0$, the free energy is identical to that of the SK model under the RS ansatz. The self-consistent equations for the order parameters q_1 , q_2 , and q_3 are given by

$$q_1 = (1 - p) \langle \tanh^2(\sqrt{\hat{q}_1}u) \rangle_0 + p \langle \tanh^2(\hat{\mu} + \sqrt{\hat{q}_1}u) \rangle_{\hat{\mu}} \quad (8)$$

$$q_2 = (1 - p) \langle \tanh(\sqrt{\hat{q}_1}u) \tanh W(u, v) \rangle_0 + p \langle \tanh(\hat{\mu} + \sqrt{\hat{q}_1}u) \tanh W(u, v) \rangle_{\hat{\mu}} \quad (9)$$

$$q_3 = (1 - p) \langle \tanh^2 W(u, v) \rangle_0 + p \langle \tanh^2 W(u, v) \rangle_{\hat{\mu}}, \quad (10)$$

where $\langle \cdots \rangle_x$ denotes the average according to the distribution (7) at $w = x$. The conjugate parameters of q_i s are given by $\hat{q}_i = \beta_S^2 q_i$ ($i = 1, 2, 3$). The first and second terms of the order parameters come from the non-target spins and the target spins, respectively. Thus, eqs.(8)–(10) can be rewritten as the summation of the non-target and the target parts, $q_i = (1 - p)q_i^{\text{nt}} + pq_i^{\text{t}}$ ($i = 1, 2, 3$). The conjugate parameter $\hat{\mu}$ is implicitly determined by the equation

$$\mu = \langle \tanh(\hat{\mu} + \sqrt{\hat{q}_1}u) \rangle_{\hat{\mu}}, \quad (11)$$

where μ is a given parameter in the fitness function and the right hand side depends on $\hat{\mu}$. The stability analysis for the RS solutions presented by de Almeida and Thouless (AT) [19] affords three conditions [20]:

$$AT_1 \equiv 1 - \beta_S^2(1 - 2q_1 + r_{11}) > 0 \quad (12)$$

$$AT_2 \equiv \left\{ 1 - \beta_S^2 \left(1 - (\beta_J + 4)q_3 + (\beta_J + 3)r_{33} \right) \right\} \\ \times \left[\beta_J + 1 - \beta_S^2 \left((\beta_J + 1)(1 - q_3) + (\beta_J - 1)(q_1 - r_{22}) \right) \right] \\ + 2\beta_J(\beta_J + 2)\beta_S^4(q_2 - r_{23})^2 > 0 \quad (13)$$

$$AT_3 \equiv 1 - \beta_S^2(1 - 2q_3 + r_{33}) > 0, \quad (14)$$

where

$$r_{11} = (1 - p)\langle \tanh^4(\sqrt{\hat{q}_1}u) \rangle_0 + p\langle \tanh^4(\hat{\mu} + \sqrt{\hat{q}_1}u) \rangle_{\hat{\mu}}$$

$$r_{22} = (1 - p)\langle \tanh^2(\sqrt{\hat{q}_1}u) \tanh^2 W(u, v) \rangle_0 \\ + p\langle \tanh^2(\hat{\mu} + \sqrt{\hat{q}_1}u) \tanh^2 W(u, v) \rangle_{\hat{\mu}}$$

$$r_{23} = (1 - p)\langle \tanh(\sqrt{\hat{q}_1}u) \tanh^3 W(u, v) \rangle_0 \\ + p\langle \tanh(\hat{\mu} + \sqrt{\hat{q}_1}u) \tanh^3 W(u, v) \rangle_{\hat{\mu}}$$

$$r_{33} = (1 - p)\langle \tanh^4 W(u, v) \rangle_0 + p\langle \tanh^4 W(u, v) \rangle_{\hat{\mu}}.$$

We introduce an expectation value for the target magnetization $m_t = [\langle \sum_{i=1}^t S_i \rangle / t]_{\beta_J}$. When $m_t = 0$, the fitness function is also equal to 0. Hence, the adaptation phase is the region satisfying $m_t > 0$. Following the replica method, the target magnetization is given by

$$m_t = \langle \tanh W(u, v) \rangle_{\hat{\mu}}, \quad (15)$$

which indicates that when $q_2 = 0$, the target magnetization is also 0. Thus, the parameter region with $q_2 > 0$ ($q_2 = 0$) corresponds to the adaptation (non-adaptation) phase, respectively.

The phase diagram on the $T_S - T_J$ plane at $p = 0.2$ is shown in Fig. 1. Here we focus our attention on the case with $\mu = 1$, and we set $\hat{\mu}$ to be sufficiently large to satisfy the self-consistent equation eq. (11) with $\mu = 1$. We define the transition temperatures $T_S^{q_2}$ and $T_S^{q_3}$ such that q_2 and q_3 are positive or zero, respectively, while q_1 takes a non-zero value at any finite T_S . At $T_J > 1$, the transition temperature $T_S^{q_3}$ is equal to 1 and the temperature $T_S^{q_2}$ is smaller than $T_S^{q_3} = 1$. Adaptation occurs at $T_S < T_S^{q_2}$, but the AT stability conditions AT_2 and AT_3 are already violated at $T_S = 1$. A preliminary Monte Carlo simulation indicates that the transition for $q_2 > 0$ and replica symmetry breaking (RSB) occurs at $T < T_S^{q_3} = 1$ [20]. At $T_J \leq 1$, $T_S^{q_2}$ coincides with $T_S^{q_3}$, while RSB occurs at a lower temperature at which $AT_3 = 0$. Thus the adaptation phase $T_S \leq T_S^{q_2}$ consists of RS and RSB phases, separated by the line $AT_3 = 0$. The RS adaptation phase is thermodynamically stable at $T_S^{\text{RSB}} < T_S < T_S^{\text{RS}}$, where T_S^{RSB} , given by $AT_3 = 0$, is the boundary between the RSB and RS phases, and T_S^{RS} is the transition temperature for q_2 and q_3 , $T_S^{\text{RS}} = T_S^{q_2} = T_S^{q_3}$. As p decreases, the region of the RS adaptation phase becomes narrower and

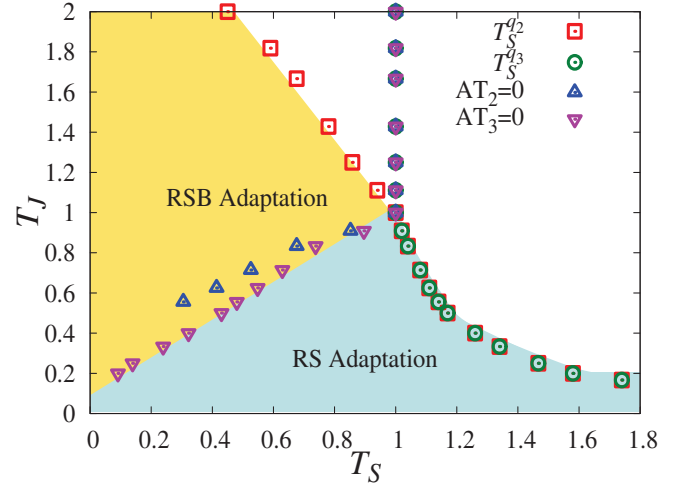


FIG. 1. (color online) Phase diagram on the $T_S - T_J$ plane at $p = 0.2$. \square and \circ indicate the transition temperatures $T_S^{q_2}$ and $T_S^{q_3}$, respectively. The adaptation phase appears in the temperature region lower than \square . \triangle and ∇ mark the boundary of the RSB phase and RS phase.

eventually the lines of $AT_2 = 0$, $AT_3 = 0$, $T_S^{q_2}$, and $T_S^{q_3}$ merge to $T_S = 1$ for any T_J at $p = 0$. In this limit, the present model is identical to the SK model whose spin-glass transition with RSB occurs at $T_S = 1$ independent of T_J .

To distinguish the interactions evolved in the RS phase from those in the RSB phase, we calculate the equilibrium frustration parameters. Indeed, the frustration characterizes the interactions in spin glasses. It is defined as the product of J_{ij} s along a minimal loop. When the interactions among the three spins satisfy $J_{ij}J_{jk}J_{ki} < 0$, the energy per spin cannot reach the minimum value, and such interactions are said to be frustrated [17, 21]. In the present model, the target spins play a distinct role because their configuration determines the fitness function. Hence, by distinguishing the target spins from others, we introduce the frustration parameters as $\Phi_1 \equiv \frac{1}{C_2^t} \sum_{i < j \leq t} [J_{ij}]_{\beta_J}$ and $\Phi_2 \equiv \frac{1}{C_2^t(N-t)} \sum_{i < j \leq t} \sum_{k=t+1}^N [J_{ik}J_{jk}]_{\beta_J}$, where C_2^t is the number of interactions between the target spins. When $\Phi_1 = 0$, the interactions between the target spins are randomly distributed; however, when $\Phi_1 > 0$, ferromagnetic interactions are dominant. The ferromagnetic interactions between the target spins energetically favor the spin configuration with $m_t = 1$. The frustration parameter Φ_2 is the average correlation of the interactions between the target and non-target spins. When the interactions that couple a non-target spin S_k to the target spins S_i and S_j satisfy the condition $J_{ik}J_{jk} > 0$, the target configuration $S_i = S_j = 1$ is stable irrespective of S_k . Therefore, the finite frustration parameter $\Phi_2 > 0$ implies that the configuration with $m_t > 0$ is energetically supported by the interactions between target and non-target interactions. Under the RS ansatz, the frustration parameters

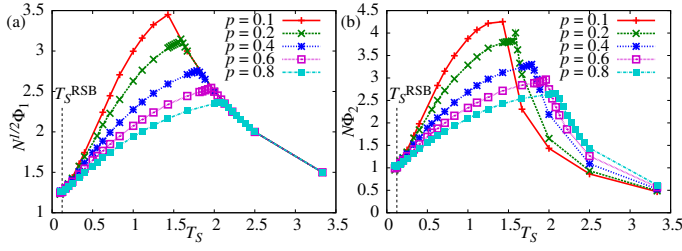


FIG. 2. (color online) T_S dependence of the frustration parameters (a) Φ_1 and (b) Φ_2 at $T_J = 0.2$. The vertical axis in (a) and (b) are rescaled with \sqrt{N} and N , respectively. The RSB transition temperature, which weakly depends on the value of p shown here, is indicated by the dashed lines.

are calculated as

$$\Phi_1^{\text{RS}} = \frac{\beta_S \beta_J}{\sqrt{N}} (\mu^2 - m_t^2) \quad (16)$$

$$\Phi_2^{\text{RS}} = \frac{\beta_S^2 \beta_J}{N} \{ (\beta_J - 1) q_1^{nt} \mu^2 - 2 \beta_J q_2^{nt} \mu m_t + (\beta_J + 1) q_3^{nt} m_t^2 + (\mu^2 - m_t^2) \}. \quad (17)$$

Here the coefficients $N^{-1/2}$ and N^{-1} reflect the change in the order of the interactions into $O(N^{-1/2})$ through the evolution [22]. As seen in Fig. 2, for any p , the frustration parameters Φ_1 and Φ_2 increase with a decrease in T_S down to $T_S = T_S^{\text{RS}}$, but with further decrease in $T_S < T_S^{\text{RS}}$, Φ_1 and Φ_2 decrease. Thus, the frustration is minimal at around the transition temperature T_S^{RS} . This result is consistent with the behavior of the energy [20]. The configurations of the interactions that evolved in the intermediate temperature range $T_S^{\text{RS}} < T_S < T_S^{\text{RSB}}$ have smaller frustration in the interactions between target spins and those between target and non-target spins.

In summary, we employed a spin-glass model of adaptive evolution to discuss evolutionary robustness in terms of statistical physics. Our analysis showed the existence

of two kinds of adaptation phases, an RS adaptation phase at $T_S^{\text{RSB}} < T_S < T_S^{\text{RS}}$ and an RSB adaptation phase at $T_S < T_S^{\text{RS}}$. The equilibrium properties of the interactions were characterized by the frustration parameters, which showed that the RS adaptation phase energetically supports the target configurations by suppressing the frustration in the evolved interactions.

Now we discuss the biological relevance of our results. An evolved system in the RS phase is robust to noise in the dynamic processes and to genetic change. The relaxation dynamics of spins progresses smoothly without becoming stuck at any metastable states. In the RS phase, the adapted phenotype, that is, the target spin configuration, is a unique stable state that is reachable from any initial conditions after a short time of relaxation. This dynamical process agrees well with that of the funnel landscape in protein folding [11, 12], as is also observed in evolution dynamics in biology [14, 15]. Next, the self-averaging property in the RS phase guarantees an identical equilibrium distribution of the phenotype even if the genotype \mathbf{J} is distributed around the evolved point. An identical phenotype is generated irrespective of genotypic variance, which is known as genetic canalization [23]. However, phenotypic robustness is lost at lower temperatures by RSB, as represented by the appearance of a continuous overlap function. Thus, our findings provide an evolutionary interpretation for RSB and also confirm a positive role for thermal noise in shaping the funnel-like dynamics and robustness to mutation.

Finally, despite the use of a simple statistical-physics model of interacting spins, we expect our findings to hold true in other problems involving evolutionary and developmental dynamics. In addition, the proposed replica formalism could function as a theoretical basis to understand the evolution of robustness in general.

This work was supported by Grants-in-Aid for Scientific Research (No. 22340109 and No. 21120004) from MEXT and for JSPS Fellows (No. 20-10778 and No. 23-4665) from JSPS.

-
- [1] D. J. Futuyma, *Evolutionary Biology (Second edition)*, (Sinauer Associates Inc., Sunderland, 1986).
 - [2] D. L. Hartl, and A. G. Clark, *Principles of Population Genetics (4th edition)*, (Sinauer Associates Inc., Sunderland, 2007).
 - [3] M. B. Elowitz et al., *Science* **297**, 1183 (2002).
 - [4] M. Kaern et al., *Nat. Rev. Genet.* **6**, 451 (2005).
 - [5] C. Furusawa et al., *Biophysics* **1**, 25 (2005).
 - [6] C. R. Laundry et al., *Science* **317**, 118 (2007).
 - [7] K. Sato et al., *Proc. Nat. Acad. Sci. USA*, **100**, 14086 (2003).
 - [8] K. Kaneko, *PLoS ONE* **2**, e434 (2007).
 - [9] A. Sakata, K. Hukushima, and K. Kaneko, *Phys. Rev. Lett.* **102**, 148101 (2009).
 - [10] S. Ciliberti et al., *PLoS Comput. Biol.* **3**, e15 (2007).
 - [11] N. Go, *Ann. Rev. Biophys. Bioeng.* **12**, 183 (1983).
 - [12] J. N. Onuchic and P. G. Wolynes, *Curr. Opin. Struc. Biol.* **14**, 70 (2004).
 - [13] L. W. Ance and W. Fontana, *J. Exp. Zool. (Mol. Dev. Evol.)* **288**, 242 (2000).
 - [14] F. Li et al., *Proc. Natl. Acad. Sci. USA* **101**, 4781 (2004).
 - [15] K. Kaneko et al., *J. Exp. Zool. B* **310**, 492 (2008).
 - [16] S. Saito et al., *Proc. Nat. Acad. Sci. USA* **94**, 11324 (1997).
 - [17] H. Nishimori, *Statistical Physics of Spin Glasses and Information Processing: An Introduction*, (Oxford Univ. Pr., 2001).
 - [18] M. Mézard et al., *Spin Glass Theory and Beyond*, (World Sci. Pub., 1987).
 - [19] J. R. L. de Almeida, and D. J. Thouless, *J. Phys. A: Math. Gen.* **11**, 983 (1978).
 - [20] A. Sakata et al., unpublished.
 - [21] G. Toulouse, *Commun. Phys.* **2**, 115 (1977).
 - [22] A. Sakata, and K. Hukushima, *Phys. Rev. E* **83**, 021105

(2011).

[23] C. H. Waddington, *The Strategy of the Genes*, (George Allen & Unwin LTD, Bristol, 1957).